THE BENTHIC MACROFAUNA OF MORICHES BAY, NEW YORK

JOEL S. O'CONNOR [1]

Biology Department, Brookhaven National Laboratory, Upton, New York 11973

The eutrophication of estuaries follows patterns that are well known in their broadest aspects but poorly known in detail.   Moriches Bay on the south shore of Long Island is a textbook example (Odum, 1959) of estuarine eutrophication. While the principal cause of eutrophication here was known to be effluent from intensive duck farming along tributaries of the bay, it was aggravated by cesspool seepage and by closure between 1951 and 1954 of the only direct access to the ocean, Moriches Inlet.   During this period the bay became anaerobic in summer, a situation that has been alleviated by dredging Moriches Inlet and by the gradual decline in duck farming.   The bay bottom, however, contains organic sediments several feet deep in some of its more eutrophic reaches.   In an effort to learn more of the details of the changes associated with eutrophication of estuaries and as a part of a longer term series of studies of the estuaries of Long Island, I have made an extensive survey of the subtidal benthic macrofauna of Moriches Bay.

Moriches Bay is a shallow lagoon located centrally along the south shore of Long Island (Fig. 1).   The lagoon is separated from the open Atlantic by the Fire Island barrier beach through which one inlet is open to the sea.   Channels also provide exchange with Great South Bay to the west and Shinnecock Bay to the east.   The lagoon is 11.4 square miles (2963 ha) in area and averages 4 feet (1.2 m) in depth.   The highly permeable drainage area of the lagoon is 80 square miles (20,720 ha).

Various aspects of the eutrophication of the bay have been examined, establishing the existence of a shift in the flora to "small forms" of phytoplankton. The blooms of these small forms was thought to have been favored by high nitrogen concentrations in reduced forms, increased temperature, and other factors (Hulbert, 1970; Ryther, 1954).   High summer concentrations of these phytoplankton were correlated with the decline of commercial oyster populations in Moriches and Great South Bays (U. S. Federal Water Pollution Control Administration, 1966a, 1966b).   It is also probable that reduced flushing of the bay resulted in the nuisance concentrations of the midge, *Tendipes attenuatus* (Walker) in the early 1950's (Jamnback, 1954; Jamnback and Collins, 1955, 1956).

During two successive summers oxygen deficits caused localized disappearance of macrofauna in the Forge River, the major tributary of Moriches Bay (Myren, 1964).   Anaerobic conditions have been sufficiently widespread to generate enough hydrogen sulfide to discolor the paint of homes adjacent to Moriches and Great South Bays (U. S. President's Science Advisory Committee, 1965), and to cause virtually the full range of effects observed under the most severe condi-

[1] Present address: Marine Sciences Research Center, State University of New York at Stony Brook, Stony Brook, New York 11790.

tions (U. S. F.W.P.C.A., 1966a, 1966b, 1967, 1968). Barlow and Myren (1961) discuss the heterotrophic nature of the Forge River in summer.

Sediments in Moriches Bay include well-sorted sands in the shallow flats around the bay margin and extending about one-third of the distance into the bay from Fire Island (Nichols, 1964). The sands grade into clayey silts which predominate in the deeper areas. Poorly sorted sand-silt-clay and silty sand "transitional" sediments occur in zones between the bay margins and deep areas. Burrowing invertebrates cause mottling of transitional and midbay clayey silt cores. Thin shell layers occurred in many of Nichols' (1964) cores and in many benthic grabs during this study. Organic deposits derived from duck farms and from the decay of plants whose growth was stimulated by nutrients from the ducks and elsewhere. These "duck sludge" deposits are often several feet deep and contain more than 10% organic matter by dry weight (Nichols, 1964). Sandy gravel and stiff clay deposits underlie Moriches Inlet but are not found elsewhere in the bay.

Eel grass (*Zostera marina*) is the dominant vegetation, covering most of the sand flats. It has a discontinuous distribution in deeper water. The annual productivity of eel grass probably approximates the average June standing crop, *i.e.*, "maximum site" biomass, of shoots in areas where it is present (1100 g/m^2) estimated by Burkholder and Doheny (1968) in Great South Bay. A variety of attached algae are abundant only in small patches. The composition of macro-algae in Moriches is similar to that of the ajoining Great South Bay which has been surveyed by Koetzner (1963).

Benthic community structure is conventionally related to environmental parameters at several stations sampled repetitively over time. This approach permits evaluation of associations between fauna and sediment properties, current speed, *etc.* However, given data from a few purposely selected stations, it is not possible to appraise the precision with which sample observations reflect the natural communities. Thus in this study samples were selected randomly in order to embrace and estimate the spatial heterogeneity so commonly acknowledged in benthic communities (Holme, 1964).

My emphasis is, therefore, upon estimating the community structure of benthic assemblages inhabiting defined biotopes. I am much less concerned with small-scale associations between benthic forms and the milieus of particular sampling stations.

Methods

Bottom samples were taken from April 1969 through June 1970 with a Ponar grab. This small sampler, equipped with additional weights, provided consistently deep grabs of approximately 0.05 m^2 surface area except in sandy sediments. The grab did not penetrate beyond 3 to 4 cm in sand (*c.f.* Powers and Robertson, 1967). The relatively unbiased nature of the Ponar grab has been discussed by Flannagan (1970), Hudson (1970) and Kajak (1971). Of the nine samplers in Flannagan's (1970, page 1699) detailed evaluation, he found, "The Ponar and Shipek grabs . . . came closest to being all-sediment samplers. . . ."

Sampling locations were selected by relating random numbers to coordinates of latitude and longitude, except 14 purposely selected samples mostly from dredged channels. Two replicate grabs were taken at each of 72 stations, and

no station was sampled more than once. Locations of the 72 sampling stations, *i.e.*, 144 grabs, are shown in Figure 1. Samples were washed through 1-mm mesh screens. All fauna were preserved in 10% buffered formalin after relaxation in propylene phenoxetol or $MgSO_4$. Each specimen was weighed individually to three significant digits after blotting dry from preservation in formalin. Mollusc shells were not weighed. Specimens of each taxon were then stored permanently in 70% alcohol. The data on frequency and weight distribution were recorded on keypunch forms. Punched data cards were then edited by a computer program and converted to magnetic tape for subsequent analyses.
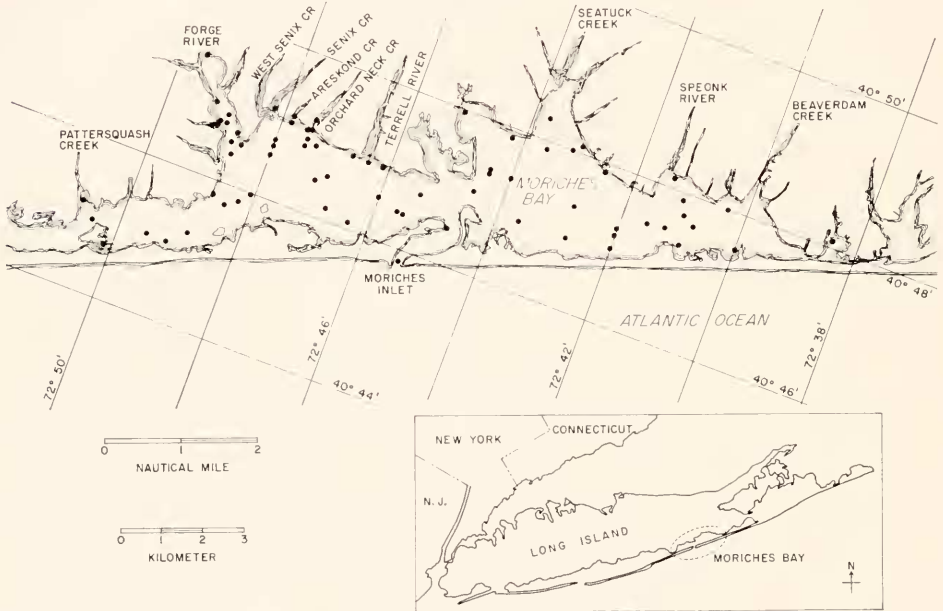

Figure 1. Locations of benthic samples taken in Moriches Bay, New York.

Replicated measurements of sediment redox potential were taken from one sandy and three transitional stations using a Beckman G pH meter with platinum and calomel electrodes.

Nomenclature follows Hartman (1959, 1965) for polychaetes, Abbott (1954) for molluscs, and Smith (1964) for all other taxa. Authors are provided for binomials not referenced by these authorities. Identifications were to species when possible. Of the amphipods, the Caprellidae only were identified to species.

Results

The 72 samples yielded evidence of five substrates that were sufficiently different among themselves to warrant recognition as separate biotopes.

Sandy sediments make up about 37% of the bay bottom. Clayey silt and silt sediments make up about 33%. Transitional sediments, *i.e.*, sand with

admixtures of from 25 to 80% clay and silt, cover about 20% of the bay bottom. Dredged channels make up the remainder, about 10%. The sandy biotope may be subdivided by distinguishing between (1) sandy sediments with dense vegetation, and (2) sand with sparse or no vegetation. Also considered separately were temporal phases of the nonsand sediments: the deeper areas with transitional, clayey silt, or silt sediments, some of which suffer prolonged oxygen depletion in summer. These potentially anoxic areas are all greater than 1 m deep, but exclude channels, and do not have appreciable tidal currents.

Bottom salinities in the open bay have ranged from 23 to 31% during the course of this study, while Moriches Inlet has remained stable since its enlargement in the spring of 1958. Salinities of less than 23% have not been encountered at any of the stations in tributaries of the bay. Bottom temperatures ranged from 0 to 27.7° C. Values above 20° C were common in July and August even

TABLE I

Numbers of individuals per m² of benthic taxa in Moriches Bay

Taxa	Sand	Transitional	Clayey silt	Dredged channels
Amphipoda	189	1253	662	87
Decapoda	22	54	15	1
Crustacea (except Amphipoda and Decapoda)	24	25	13	17
Gastropoda	462	541	269	19
Pelecypoda	4136	486	76	6
Tunicata	—	5	50	—
Polychaeta	557	501	317	267
Turbellaria	1	<1	—	—
Nemertea	8	11	12	2
Insecta	—	—	5	—
Echinodermata	—	—	<1	—
Holothuroidea	3	5	13	—
Balanoglossida	—	1	—	—
Total	5402	2978	1433	399

in the deepest areas. Rather large areal variations in temperature and salinity result from tidal mixing and discontinuous groundwater seepage through the bay bottom. Groundwater seepage through the bay bottom is the primary freshwater source (U. S. F.W.P.C.A., 1966b).

Table I indicates the estimated abundance, in numbers per square meter, of the major taxa. A complete list of all benthic species encountered in 144 replicated Ponar grabs is available from: ASIS–National Auxiliary Publications Service, c/o CCM Information Corp., 909 Third Ave, New York, New York 10022. While the proportionate taxonomic representation is comparable to other studies, the absolute densities are appreciably lower than typical observations in temperate estuaries, *e.g.*, Raymont (1949), Sanders (1956), Phelps (1964), and Ellis (1967). It is also clear that dredged channels have a particularly sparse fauna in contrast with any other biotope. Murawski (1969) also found a dearth of invertebrate fauna in dredged areas of New Jersey estuaries.

The wet weights of major taxa are given in Table II. Bivalves contribute most of the wet weight biomass in sand and transitional sediments, *i.e.*, in over

TABLE II

Biomass (wet weight, g/m²) of benthic taxa in Moriches Bay

Taxa	Sand	Transitional	Clayey silt	Dredged channels
Amphipoda	1.2	3.0	1.7	0.3
Decapoda	2.1	1.6	2.0	—*
Crustacea (except Amphipoda and Decapoda)	0.3	0.3	0.1	0.1
Gastropoda	3.0	5.3	0.7	0.1
Pelecypoda	36.1	49.9	7.3	0.1
Tunicata	—	0.9	15.8	—
Polychaeta	5.5	10.6	17.7	3.5
Turbellaria	<0.1	<0.1	—	—
Nemertea	0.1	0.1	0.2	<0.1
Insecta	—	—	<0.1	—
Echinodermata	—	—	0.2	—
Holothuroidea	0.5	<0.1	0.3	—
Balanoglossida	—	<0.1	—	—
Total	58.9	71.9	46.1	4.2*

* Excludes one large *Cancer irroratus* weighing 35 g, wet weight.

57% of the bay bottom. In clayey silts the Polychaeta predominate. While tunicates contribute almost as much wet weight in clayey silt, they are much less significant in terms of dry weight or energy transfer than are polychaetes, or even bivalves.

Most ash-free dry weights were estimated by using the averages of conversion values given by Thorson (1957) and Lie (1968). Similar conversion values for tunicates were determined by the author.

The most useful illustration of biomass composition from the standpoint of carbon bound by the benthos is given by ash-free dry weights of the major taxa

TABLE III

Biomass (ash-free dry weight, g/m²) of benthic taxa in Moriches Bay

Taxa	Sand	Transitional	Clayey silt	Dredged channels
Amphipoda	0.21	0.52	0.31	0.06
Decapoda	0.36	0.28	0.35	—*
Crustacea (except Amphipoda and Decapoda)	0.05	0.05	0.01	0.02
Gastropoda	0.24	0.41	0.05	0.01
Pelecypoda	2.21	3.05	0.44	0.01
Tunicata	—	0.01	0.16	—
Polychaeta	0.89	1.71	2.86	0.56
Turbellaria	<0.01	<0.01	—	—
Nemertea	0.01	0.01	0.03	<0.01
Insecta	—	—	<0.01	—
Echinodermata	—	—	0.01	—
Holothuroidea	0.04	<0.01	0.02	—
Balanoglossida	—	<0.01	—	—
Totals	4.02	6.07	4.25	0.66*

* Excludes one large *Cancer irroratus* weighing about 6 g, ash-free dry weight.

TABLE IV

Biomass (wet weight, g/m²) of dominant species in Moriches Bay. Species listed in order of dominance by weight. Upper list contains species with average biomass ≥ 0.5 g/m² in any major sediment classification. Lower list contains less dominant species averaging ≥ 10 individuals/m² in any major sediment classification

Species	Sand	Transitional	Clayey silt	Moderate to dense vegetation	Sand w/o much vegetation	Summer oxygen depletion	Lack of, or recovery from, oxygen depletion	Dredged channels
Mercenaria mercenaria	25.5	36.3	1.6	11.3	34.0	<0.01	0.8	—
Mytilus edulis	4.7	8.2	—	8.4	<0.1	—	0.1	<0.1
Clymenella torquata	0.9	3.9	5.1	1.0	0.7	0.5	5.6	—
Bostrichobranchus pilularis	—	—	8.0	—	—	—	—	—
Molgula provisionalis	—	<0.1	7.8	0.1	—	0.1	0.1	—
Nereis succinea	0.3	0.6	4.1	0.4	0.3	1.1	1.2	—
Nassarius obsoletus	1.1	3.7	—	7.8	0.2	—	4.1	—
Glycera americana	<0.1	1.8	2.2	0.1	—	0.3	1.9	—
Gemma gemma	3.4	<0.01	<0.1	<0.1	6.0	<0.01	<0.1	—
Tellina agilis	1.3	1.4	0.3	0.7	1.8	0.3	0.6	—
Neopanope texana	1.5	0.8	0.3	3.3	0.1	—	0.7	—
Pitar morrhuana	—	2.1	2.6	—	—	—	2.7	—
Heteromastus filiformis	<0.1	0.2	1.9	<0.1	0.1	3.7	0.2	<0.1
Laevicardium mortoni	0.5	0.6	0.8	0.9	0.5	<0.1	0.4	—
Mulinea lateralis	0.1	0.4	1.4	—	0.1	0.5	1.1	0.1
Scoloplos robustus	0.4	0.6	0.7	0.5	0.3	0.9	0.3	—
Scoloplos acutus	0.6	0.2	0.3	—	0.3	0.2	0.3	<0.01
Callinectes sapidus	—	<0.01	1.5	<0.01	—	<0.1	<0.01	—
Nereis virens	0.5	—	0.5	1.0	—	1.1	—	—
Pectinaria gouldii	0.1	0.9	0.4	0.1	0.1	0.3	0.5	0.2
Urosalpinx cinerea	0.8	0.2	—	1.7	0.1	—	0.2	<0.1
Platynereis dumerilii	0.5	0.3	<0.1	1.3	<0.1	<0.1	0.3	—
Crangon septemspinosa	0.5	0.2	0.1	0.7	0.2	—	0.1	—
Botryllus schlosseri	—	0.7	—	1.1	—	—	0.8	—
Retusa canaliculata	0.1	0.4	0.4	0.1	0.1	0.4	0.4	<0.1
Capitella capitata	0.3	<0.1	0.3	<0.1	0.5	—	0.2	3.1
Nereis arenaceodonta	0.2	0.1	0.1	0.3	0.2	<0.1	0.1	—
Haminoea solitaria	<0.1	0.3	0.2	<0.1	—	0.2	0.2	—
Mitrella lunata	0.3	0.2	<0.1	0.8	<0.1	—	0.1	<0.01
Bittium alternatum	0.3	0.3	0.1	0.7	<0.1	<0.01	0.2	—
Solemya velum	0.2	0.2	0.1	0.3	—	0.2	0.1	—
Idotea baltica	0.2	<0.1	—	0.3	—	—	—	—
Hydrobia totteni	0.1	<0.01	<0.01	<0.1	0.2	—	<0.01	—
Goniadella gracilis	0.1	0.1	0.1	<0.1	0.1	0.1	0.1	—
Polydora ligni	<0.1	0.1	<0.1	0.1	0.1	0.1	<0.1	—
Polycirrus medusa	0.1	<0.1	—	<0.01	<0.01	<0.01	<0.1	—
Number of samples	23	21	17	13	13	8	19	9

(Table III). Measured as ash-free dry weight, polychaetes are relatively more important because they contain more than twice the organic carbon per unit wet weight found in molluscs. Considering the bay as a whole, polychaetes and bivalves predominate in units of ash-free dry weight, with 41 and 36%, respectively, of the total benthic dry weight.

A rather striking feature of benthic structure is the low value of average dry weight. The mean ash-free dry weight of < 5 g/m² is rather evenly distributed among the three main sediment types (Table III).
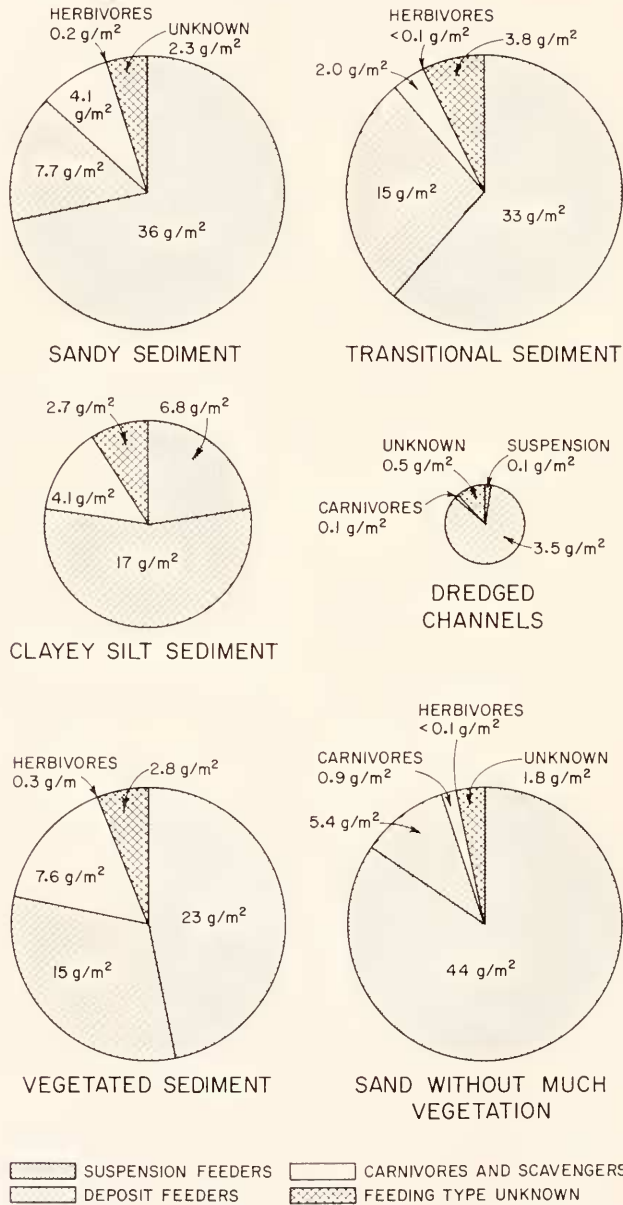

FIGURE 2. Relationships between sediment types and biomass (g/m², wet weight) of benthic feeding types. Areas of the circles are proportional to total wet weight biomass.

Table IV enumerates the biomass estimates of dominant species encountered. The large rarer specimens of the hard clam (*Mercenaria mercenaria*), blue mussel (*Mytilus edulis*) and other species induce great variability in these biomass estimates. The number of samples taken and their random selection do not insure usefully precise indications of biomass, even for the dominant species. Considerations of sampling precision will be taken up in another paper.

To help assess the influence of oxygen concentration on the benthos, a set of samples were characterized as probably suffering from prolonged summer oxygen deficits. Redox potentials in the upper 2 cm of three such stations averaged −236 mv, indicating anoxic conditions. Benthic samples taken from July through September were compared with stations of the same sediment types which either do not suffer oxygen deficits, or had some time to recover from summer oxygen depletion. While most of the latter ("recovering") stations probably underwent

TABLE V

Numbers/m² and ash-free dry weights/m² of benthic taxa from stations with, and without, low oxygen concentrations. All stations are from transitional, clayey silt, or silt sediments

Taxa	During oxygen depletion		Aerobic or partially recovered	
	No./m²	Dry wt./m²	No./m²	Dry wt./m²
Amphipoda	612	0.25	420	0.25
Gastropoda	228	0.05	527	0.43
Pelecypoda	90	0.18	79	0.36
Polychaeta	307	1.48	283	1.97
All other taxa	35	0.12	57	0.21
Total	1271	2.08	1365	3.21

oxygen depletions during summer, they were sampled from January through June, thereby allowing recolonization by the benthos for periods of 4 to 10 months. All samples compared were from transitional or clayey silt sediments over 1 m deep.

Numerical abundances of the higher taxa are roughly the same at both aerobic and recovering stations, but there seems to be more biomass within the aerobic environments. Thus the individuals of most major taxa have greater average weights at the aerobic and recovering stations.

Over 90% of the wet weight biomass could be classified by feeding type. The taxa within each sediment type were defined as suspension or deposit feeders, carnivores plus scavengers, or herbivores, *i.e.*, feeding on macro-algae, eel grass or epiphytes. The weight of any species having two or more modes of feeding was equally divided among the modes. Figure 2 illustrates the marked transition from dominance of suspension feeders in the sandy sediments to dominance by deposit feeders in the fine sediments and in dredged channels.

Species diversity indices of all benthic taxa, except Amphipoda, were calculated for each biotope. The index used was derived from information theory ($H = 1/N$ ($\log_2 N! - \Sigma \log_2 N_i!$) where N = number of all individuals in a sample and N_i = number of the i'th species. The average H for dredged

channels was 1.3 (SE = 0.41) as opposed to a mean value for the rest of the bay of 4.6 (SE = 0.25).

DISCUSSION

The low standing crop of benthos in Moriches Bay (< 5 g/m², ash-free dry weight) appears to be less than crops observed in areas with less primary production than Moriches Bay. Perhaps the most comparable area is the small coastal lagoon in Scotland studied by Raymont (1947, 1949). Estimates of primary production are apparently not available for this area, but estimates of benthic standing crop (using 1-mm mesh screens also) rose from about 4 g ash-free dry weight per square meter to a maximum of 20 g after 2 years of artificial fertilization (Raymont, 1949). The data from Sanders (1956) have been com-

TABLE VI

Moriches Bay estimated annual net primary productivity

	Area (ha) represented	Total dry wt productivity (kg/ha, yr)	Total productivity (kg C/yr) ($\times 10^5$)	kg C ($\times 10^5$) in bay proper
Phytoplankton	2963	11.6×10^6	16.4*	16.4
Eel grass (shoots only)	593	6.8×10^6	24.7†	24.7
Marshes (aboveground productivity)				
Spartina alterniflora	1141	6.3×10^6	25.0†	11.3
S. patens	570	7.7×10^4	0.3†	0.1
Distichlis spicata	570	9.9×10^4	0.4†	0.2
				gC/m² in bay proper: 177.8

* Using: kg C = 0.14 $\times$ total dry wt. (or "algal wt"). A high value within Strickland's (1960) range of conversion factors (0.09–0.15) is used because most of the Moriches Bay phytoplankton lack high concentrations of calcareous or siliceous material.

† Conversions employed the proximate analyses of Udell *et al.* (1969) and the carbon content of organic compounds given by Westlake (1963).

bined to estimate ash-free dry weights for all sizes of benthic forms in Long Island Sound. He appropriately warns of the variability introduced by large invertebrates, but his data are the most extensive available for the Sound. Including all species found by Sanders (1956), estimates of ash-free dry weight range from 8 to 41 g/m² (excluding extreme observations at 3 stations). In evaluating this contrast between Long Island Sound and Moriches Bay, the relative sampling bias of the Ponar grab and the modified 'Forster' anchor dredge used by Sanders must be kept in mind, but this bias has not yet been evaluated. The best estimate of annual net primary productivity in Long Island Sound is probably 43.9 gC/m² (Yentsch, 1963).

Any comparative estimate of annual primary productivity for Moriches Bay is imprecise, but perhaps as precise as the above estimate for the Sound. The estimates of productivity in a portion of Great South Bay by Udell, Zarudsky, Doheny, and Burkholder (1969) can be adapted to Moriches Bay for our purposes. Udell *et al.* (1969) found net annual phytoplankton productivity to be 3942 g dry matter per square meter. Where eel grass was present its net pro-

ductivity was 1142 g/m², dry weight. Comparable productivity values for marsh grass stems were: *Spartina alterniflora*, 549 g/m²; *S. patens*, 502 g/m²; and *Distichlis spicata*, 645 g/m². Table VI illustrates the estimated net annual productivity of Moriches Bay proper, assuming 45% of the aboveground marsh productivity is exported to the subtidal areas of the bay as degraded organic matter and bacteria, as found by Teal (1962) in a Georgia salt marsh. The area of marsh adjoining Moriches Bay, and its dominant plant composition, was kindly provided by Mr. Roy Haje, New York State Department of Environmental Conservation, from a review of aerial photographs and correlated field surveys.

To the 178 gC/m² annual net productivity calculated in Table V must be added the carbon enrichment by duck farm effluent. Perhaps the single most useful measure of duck farm effluent is total BOD contributed to the Bay. During most of the recent life of the Bay (1940–1965) an average of about 1.4×10^6 kg BOD/yr have been flushed into Moriches Bay from duck farms (U. S. F.W.P.C.A., 1966). This is equivalent to 1.4×10^5 g BOD/m²/yr, on average, but most of this organic loading is concentrated during the summer months and it is not evenly distributed in the Bay. Since 1965 efforts have been made to reduce the organic and nutrient loading by installing aeration lagoons and settling ponds. Recently available data from Mr. Kenneth Johanson, Cornell University Duck Research Laboratory, indicates that the annual BOD loading from duck farms has been reduced to about 3.3 g/m² during 1970. Thus it seems clear that in the recent past, the benthos of Moriches Bay have had much more bound carbon available to them than the benthos of other environments discussed above.

The lower average weight of individuals at stations under oxygen stress (Table V) is consistent with the hypothesis that, throughout much of the deeper sediment summer oxygen deficits kill many benthic species or at least retard their growth rates. It is also likely that these areas with low oxygen concentrations are annually recolonized by larval forms of a few species (Table IV). It is also clear from Table IV that *Heteromastus filiformis* is the only species clearly exhibiting greater biomass in the anaerobic sediments. This species is similar anatomically and probably physiologically to the closely related *Capitella capitata*. *C. capitata* is widely recognized as a cosmopolitan species tolerant of, and often flourishing under, oxygen stress (Reish, 1955, 1957, 1959; Felice, 1954; Henriksson, 1969). Conversely, a number of species which are intolerant of oxygen stress are more abundant at the aerobic and recovering stations, *e.g.*, *Nassarius obsoletus*, *Pitar morrhuana*, and *Clymenella torquata* (Table IV).

Despite the influence of oxygen tension, a number of additional factors almost certainly conspire to suppress benthic standing crops, perhaps synergistically with oxygen depletion. Large scale shifting of sediment was noted during the course of this study. It seems likely that such agitation and sediment deposition could destroy at least the newly settled stages of many species (Rhoads and Young, 1970). There are also substantial layers of dead shell widely distributed in deeper waters. These shell layers could interfere with the establishment of infauna, as suggested by Sanders (1956) at one of his Long Island Sound stations. Residues of DDT were found in concentrations of 0.28 lbs/acre (0.31 kg/ha) in subtidal sediments and 13.1 lbs/acre (14.7 kg/ha) in *Spartina* mats at the edge of Great South Bay (Woodwell, Wurster and Isaacson, 1967). The marshes ad-

joining Moriches Bay have been treated with DDT under the same mosquito control program. The impact of such DDT levels upon fiddler crabs (*Uca pugnax*) has been studied by Odum, Woodwell and Wurster (1969) and the possible selective uptake of toxins such as DDT adsorbed to clays and silts, particularly by nonselective deposit and suspension feeders, has been discussed by Carriker (1967). It is possible that DDT and other toxins have contributed to the inhibition of benthic production, particularly of carnivores and nonselective detritus feeders. The degree of predation within the benthic communities and by fishes and birds is unknown. However, Blegvad (1928) and Raymont (1947) have provided convincing evidence for measurable fish predation upon estuarine benthic communities.

The dominance of suspension feeders in sandy environments and dominance of deposit feeders in fine sediments has already been discussed by Sanders (1958), Rhoads and Young (1970), and others. Lacking information on the amount and quality of resuspended sediment, it is not possible to clearly ascribe this relation-

TABLE VII

Qualitative comparison of mollusc species abundance in 1938 and 1969–70

Common to abundant in 1938, now rare	Common to abundant in 1969–70, rare in 1938
Acteon punctostriatus	*Bittium alternatum*
Eupleura caudata	
Nassarius trivitattus	
Crassostrea virginica	*Mulinia lateralis*
Mya arenaria	*Tellina agilis*
Nucula proxima	

ship in Moriches Bay either to a paucity of food for suspension feeders over fine sediments, as suggested by Sanders (1958) or to the several influences of instability in the biogenically reworked sediments as described by Rhoads and Young (1970).

It is clear that biogenic reworking of fine sediments in Moriches Bay is not done by the influential bivalves described by Rhoads and Young (1970) in Buzzards Bay. These species, *Nucula proxima, Macoma tenta,* and *Yoldia limatula,* are either rare or not found in Moriches Bay. In fact, the only two bivalves, with estimated densities greater than 15 individuals/m² in clayey silt are *Tellina agilis* and *Mulinea lateralis; Tellina* only being a deposit feeder. Several abundant polychaetes are undoubtedly responsible for biogenic reworking in Moriches Bay: *Clymenella torquata, Pectinaria gouldii,* and several of the Capitellidae.

Historical comparisons

A benthic survey of Moriches Bay and other Long Island estuaries is summarized by Townes (1939). Because this early survey provides only qualitative information, it is possible to detect only striking changes in benthic species composition. Differences in abundance of polychaetes are not considered because of possible confusion introduced by misclassification. It is possible to determine with

reasonable certainty, however, changes in abundance of several molluscs (Table VII).

The decline of the eastern oyster (*Crassostrea virginica*) is documented from catch statistics (Nassau-Suffolk Regional Planning Board, 1966). The oyster decline is not clearly attributable to any single factor. Blooms of nannoplankton in the 1950's clogged the gills of oysters, reducing their production and market quality. However, the commercial concentrations of oysters in Moriches and Great South Bays had been maintained for many years by the commercial transplantation of spat from other areas. Commercial oyster transplantation also ceased in the late 1950's. The disease MSX was also identified as a cause of oyster mortality in the 1960's, and may have been present long before its identification. It is likely that the thick-lipped drill (*Eupleura caudata*) declined because it relied upon the oyster for food. The almost complete absence of soft-shell clams (*Mya arenaria*) is somewhat unexpected since they can tolerate rather high loads of organic matter (Henriksson, 1969). While it is possible that large individuals burrowed deeper than my grab penetrated in sand, it seems certain that many more small specimens would have been found if soft clams were abundant.

The increase in abundance of *Bittium alternatum* since 1938 is probably associated with the widening distribution of eel grass since its decline in the 1930's. Stauffer (1937) has emphaszied the close association between eel grass and *B. alternatum* on the Massachusetts coast. *Mulinia lateralis* seems more successful in clayey silt and silt sediments than is indicated in the Long Island Sound data of Sanders (1956). This fast-growing, short-lived species probably has widely fluctuating densities from year to year, particularly at specific locations.

Species diversity

Several explanations for spatial and temporal differences in benthic diversity have been summarized by Sanders (1968).

Pielou (1966) has pointed out that the Shannon and Weaver (1963) average diversity index ($H' = - \Sigma p_i \log_2 p_i$, where p_i is the proportionate abundance of the i'th species) is independent of sample size if the sampled area is truly representative of the community from which it was taken. I am not aware of any benthic studies which estimate the proportionate abundance of essentially all species in a community well enough to justify strictly the use of Shannon and Weaver's (1963) index, which may be viewed as an approximation of Brillouin's (1962) information measure:

$$H = 1/N \ (\log_2 N! - \Sigma \log_2 N_i!)$$

when each N_i (number of the i'th species) is large enough to permit use of Sterling's approximation to the logarithm of a factorial. Pielou (1966) also points out the typical problem, in practice, of bias in the average diversity (H') due to a number of small N_i, even if the proportionate abundance of rare species is accurately estimated.

Thus H was calculated (as preferable to H') for several biotopes of Moriches Bay. Exact values of $\log_2 N!$ and $\log_2 N_i!$ were calculated for values of $N \leq 175$; Sterling's approximation being used for larger values. Comparisons were made between means of sample H values from sand, transitional, clayey silt, summer

samples from clayey silt and transitional areas with summer oxygen depletion, samples from these areas after at least four months of recovery from oxygen deficits, and dredged channels. The Student–Newman–Keuls test for multiple comparisons (Sokal and Rohlf, 1969, pages 242–246) was used to test for differences between means of H from these biotopes. The diversity of dredged channels was significantly less ($P < 0.05$) than each other biotope, but no significant differences were detected between any two of the other biotopes.

This inability to detect significant differences in species diversity among sediment types raises an important question. How powerful is the significance test used? That is, what is the probability of finding biologically meaningful differences in diversity if they really exist? This risk, or error, was evaluated using:

$$n \geq 2 \, (\sigma/\delta)^2 \, \{t_{\alpha[v]} + t_{2(1-P)[v]}\}^2$$

as given by Sokal and Rohlf (1969, pages 246–249) where: $n =$ number of replicates; $\sigma =$ true standard deviation $\simeq s = 1.81$ in this study; $\delta =$ the smallest true difference that it is desired to detect, taken to be 1.38 in this study, i.e., the observed difference between means of H in transitional and clayey silt biotopes; $v =$ degrees of freedom of $s = 59$ in this study; $P \; (=\beta)$ i.e., the desired probability that a difference as small as δ will be found to be significant; $t_{\alpha[v]}$ and $t_{2(1-P)[v]} =$ values from a two-tailed t table with v degrees of freedom and corresponding to probabilities of α and $2(1-P)$, respectively. Given the effort in this study of 62 replicated samples, the β error is $> 60\%$, i.e., the probability is less than 0.4 that we will detect (at $\alpha = 0.05$) a difference between two sediment types of $\Delta H = 1.38$ which is presumed to exist. To reduce this β risk to 0.2, it would have been necessary to take 84 replicated samples.

As in most ecological field studies, my limitation to 62 replicated samples was dictated almost entirely by the practical consideration of available manpower, not by a priori assessment of the likelihood of answering particular questions. This is a serious flaw in many ecological studies. It is clearly evident in this study, if a real difference of 1.4 between the diversity of two biotopes is judged biologically meaningful. Thus it seems likely that if benthic studies are to critically assess species diversity (and other structural parameters of communities) they must employ appreciably more sampling effort than is typical of benthic studies. (The further importance of well-designed sampling strategies is even more evident.)

Because of obvious differences among studies such as various screen mesh sizes, sampling gear, etc., it is not possible to compare the species diversity of Moriches Bay with most other studies. Differences in sampling strategy also make comparisons difficult or impossible; the expected variance of H from randomly selected samples, as taken in this study, will be higher than the variance of repeated samples from a few fixed stations. Indeed, it is typically impossible to compare with any confidence the diversity of samples from natural communities, given repeated samples at purposely-selected stations, because the sample variance will inevitably underestimate the population variance.

Despite the lack of comparability between this study and all others it seems likely that the species diversity of Moriches Bay is somewhat higher than that of a Rhode Island coastal lagoon studied by Phelps (1964). Phelps' diversity values (calculated as H′) averaged 2.1 in "mud" and 2.8 in sand. Since his

sample sizes (0.13 m²) were essentially the same as used in this study, and since he used 0.5-mm mesh screens as opposed to the 1-mm mesh used here, his expected sample values of H would average larger than mine if the two areas had the same species composition. Phelps also identified species of all amphipods, whereas I identified only the caprellids, which should even further increase his diversity estimates. Thus, Moriches Bay diversity values ($\overline{H} = 4.6$) are significantly higher ($P < 0.001$, using Student's t test) than those of Phelps (2.4) if the sample variance of H in Phelps' lagoon is identical to that of Moriches Bay.
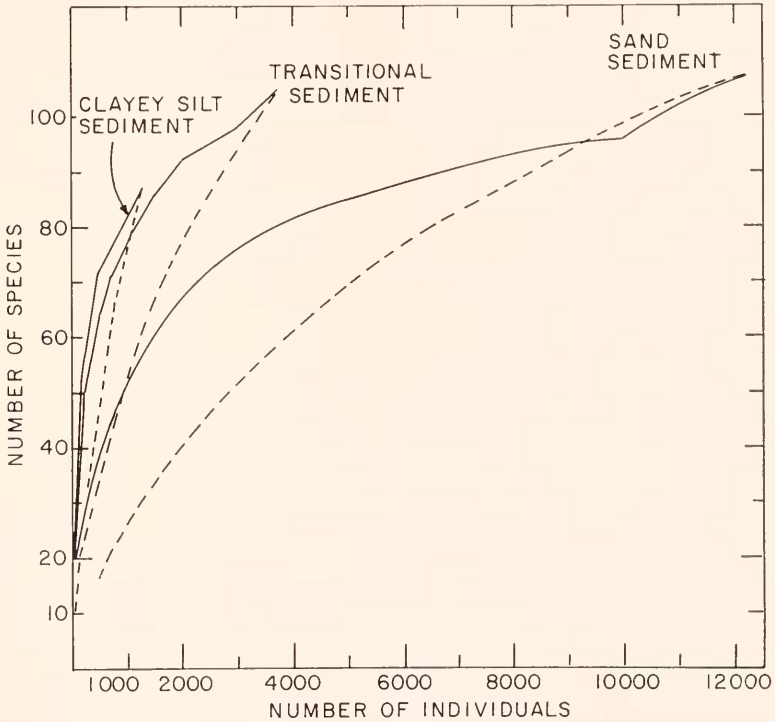
FIGURE 3.   Rarefaction curves (———) and empirically derived "species/individuals" curves (– – – –) for all taxa sampled in Moriches Bay. Amphipods, except Caprellidae, are not included.

Sanders' (1968) rarefaction index of species diversity has also been calculated for all species encountered in Moriches Bay (Fig. 3). It must be noted that the algorithm given by Sanders (1968) for his rarefaction curve results in higher numbers of species at almost all frequencies of individuals than are actually experienced in sampling. This is because Sanders' rules for generating rarefaction curves result in consistent overestimates of the numbers of species encountered at all levels of sampling intensity except near both extremes of a rarefaction curve. This feature of rarefaction curves does not rule out their use as indices of diversity, but the curves do not strictly portray the regression of numbers of species encountered on numbers of individuals sampled. Thus, as

shown in Figure 3, the rarefaction curves are consistently above the corresponding curves calculated from the averages of species and individuals found in all possible combinations of samples taken 1, 2, 3, *etc.*, at a time. These latter curves, are identical with the classical "species/area" curves widely used in ecology; the units of the abscissa in Figure 3 are simply average number of individuals per (cumulative) unit of area. The units of the abscissa could as well be cumulative area sampled, without changing the coordinates of the curve at all. Thus the curves of Figures 3 and 4 are called "species/individuals" curves without any implication that they are yet another diversity measure. It is also clear that neither these curves nor rarefaction curves are independent of sample size
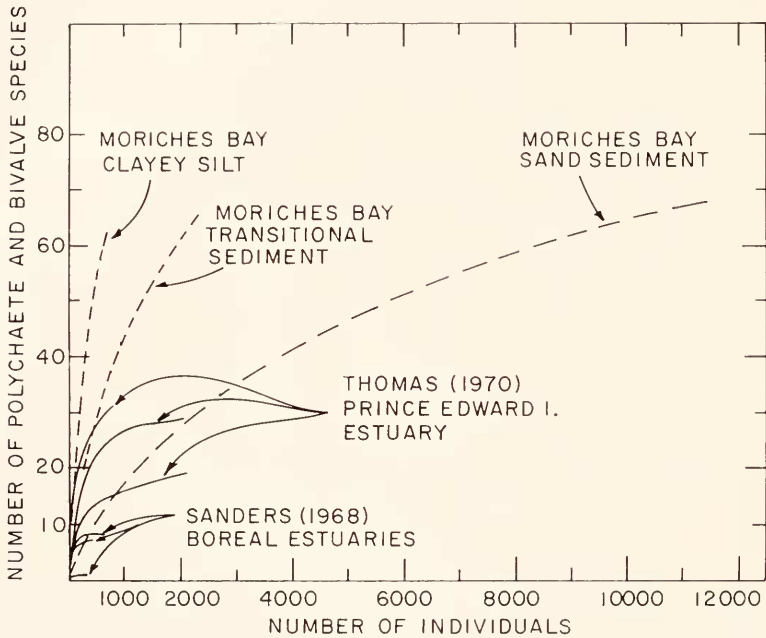

FIGURE 4. Rarefaction curves (———) and empirically-derived "species/individuals" curves (– – – –) for bivalves and polychaetes.

(Greig-Smith, 1964, page 151). While techniques are not available for statistical comparison of either measure of diversity shown in Figure 3, most of the difference between the curve for sand sediments and those of other sediment types is due to the preponderance of *Mytilus edulis* and *Gemma gemma* in sand samples (9686 individuals, or 79% of all specimens from sand samples).

Since Sanders' (1968) rarefaction curves, and those of Thomas (1970) include bivalves and polychaetes only, a comparison of rarefaction and "species/individuals" curves for these taxa is given in Figure 4. The Moriches Bay curves in this figure are much steeper than those of both Sanders and Thomas from boreal estuaries, primarily because my study employed random sampling of species almost always contagiously distributed, in contrast to the repetitive sampling at fixed stations by Sanders (1968) and Thomas (1970). It is important to note

that the rarefaction method was designed as a measure of "within-habitat" diversity (Sanders, 1968, page 243). That is rarefaction curves have been generated by Sanders and others from samples within rather homogeneous species assemblages. Rarefaction curves will differ from "species/individual" (or species/area) curves less as the sample universe becomes more homogeneous. Indeed, when all samples are from essentially the same location, the resultant species/individuals and rarefaction curves should differ very little. Sanders and his colleagues are currently exploring the question in more detail. Thus no diversity comparisons are made between this study and the diversity of Buzzard's Bay studied by Sanders, or of Bideford River, Prince Edward Island, studied by Thomas.

Unsatisfactory results were found in attempting to trace the seasonal growth patterns of even dominant species. While this technique has been used by Sanders (1956) to estimate benthic productivity and by Lie (1968) to estimate the growth rates of some benthic species in Puget Sound, I was unable to estimate growth rates of any species. Given the sample-processing effort expended in this study (about one man-year) I question the desirability of expending the effort required to estimate species-specific productivity rates of the benthic macrofauna by this method in species-rich estuaries.

Summary

Quantitative sampling of the subtidal macro-benthos of a shallow temperate lagoon shows several structural features of benthic communities in five biotopes. Attempts are made to relate past and present qualities of benthic structure to long-term nutrient and organic loading of this lagoon. While overall benthic species composition has apparently not changed drastically since a 1938 qualitative survey, some important changes in dominant species composition appear to be associated with the biology of these principal species. The best estimate of average annual standing crop of the macro-benthos (< 5 g/m², ash-free dry weight) is lower than estimates in somewhat comparable estuaries, apparently because of low oxygen concentrations over extensive areas during summers, which derive in turn from large summer influxes of nutrients and organic matter into this poorly flushed lagoon. Clear-cut associations between sediment type and mode of feeding of the benthos are demonstrated; suspension feeding invertebrates dominating in sandy sediments, and deposit feeders dominating in soft clayey silt bottoms. Species diversity appears to be homogeneous over most of the bay, with very low diversity in dredged channels. The need for more, and

more carefully allocated, sampling effort in benthic studies is emphasized, given the imprecision in community structural features, particularly species diversity and biomass of genera and species.

LITERATURE CITED

ABBOTT, R. T., 1954. *American Seashells.* D. Van Nostrand, Princeton, New Jersey, 541 pp.

BARLOW, J. P., AND R. T. MYREN, 1961. Oxygen resources of tidal waters. *Water Sewage Works,* **109**: 68–72.

BLEGVAD, H., 1928. Quantitative investigations of bottom invertebrates in the Limfjord 1910–1927 with special reference to plaice food. *Rep. Dan. Biol. Sta. Min. Agr. Fish.,* **34**: 33–52.

BRILLOUIN, L., 1962. *Science and Information Theory.* [2nd edition] Academic Press, New York, 320 pp.

BURKHOLDER, P. R., AND T. E. DOHENY, 1968. *The Biology of Eelgrass.* Contrib. No. 3, Dept. of Conservation and Waterways, Town of Hempstead, Long Island, New York, 120 pp.

CARRIKER, M. R., 1967. Ecology of estuarine benthic invertebrates: A perspective. Pages 442–487 in G. H. Lauff, Ed., *Estuaries.* American Association for the Advancement of Science, Washington, D. C.

ELLIS, D. V., 1967. Quantitative benthic investigations. I. Satellite channel biomass summaries and major taxon tank orders, Feb. 1965–May 1967. *Fish. Res. Board Can., Tech. Rept., No.* **25**: 1–49.

FELICE, F. P., 1954. An ecological survey of the Castro Creek area in San Pablo Bay. *Wasmann J. Biol.,* **12**: 1–24.

FLANNAGAN, J. F., 1970. Efficiences of various grabs and corers in sampling freshwater benthos. *J. Fish. Res. Board Can.,* **10**: 1691–1700.

FOEHRENBACH, J., 1969. Pollution and eutrophication problems of Great South Bay, Long Island, New York. *J. Water Pollut. Contr. Fed.,* **41**: 1456–1466.

GREIG-SMITH, M. A., 1964. *Quantitative Plant Ecology.* [2nd edition] Butterworths, London, 256 pp.

HARTMAN, O., 1959. Catalogue of the polychaetous annelids of the world, Parts I and II. *Allan Hancock Found. Publ. Occas. Pap.,* **23**: 1–628.

HARTMAN, O., 1965. Catalogue of the polychaetous annelids of the world, Supplement 1960–1965 and Index. *Allan Hancock Found. Publ. Occas. Pap.,* **23**: 1–197.

HENRIKSSON, R., 1969. Influence of pollution on the bottom fauna of the Sound (Oresund). *Acta Oecol. Scand.,* **20**: 507–523.

HOLME, N. A., 1964. Methods of sampling the benthos. Pages 171–260 in F. S. Russell, Ed., *Advances in Marine Biology, Vol. II.* Academic Press, London and New York.

HUDSON, P. L., 1970. Quantitative sampling with three benthic dredges. *Trans. Amer. Fish. Soc.,* **99**: 603–607.

HULBERT, E. M., 1970. Competition for nutrients by marine phytoplankton in oceanic, coastal, and estuarine regions. *Ecology,* **51**: 475–484.

JAMNBACK, H., 1954. The Biology and Control of the Midge *Tendipes decorus* (Joh.) in Moriches Bay. *Preliminary Report, Report of Investigation,* No. **6**: (Available from New York State Science Service, The University of the State of New York, Albany, New York 12203.]

JAMNBACK, H., AND D. L. COLLINS, 1956. Continued studies of fuzz-bill *Tendipes decorus* (Joh.) control on Long Island In: *Proc. 43rd Ann. Mtg., New Jersey Mosquito Extermination Ass.,* March 7–9, 1956, Atlantic City, New Jersey.

JAMNBACK, H., AND D. L. COLLINS, 1955. The probable correlation between increasing salinity and the disappearance of the gnat *Tendipes decorus* (Joh.) from Moriches Bay. In: *Proc. Pap. 23rd Annu. Conf. Calif. Mosquito Contr. Ass.,* 1955.

KAJAK, Z., 1971. A review of methodology in benthic sampling. In W. T. Edmondson, Ed., *The IBP Handbook Series.* Blackwell, Scientific Publications, Oxford and Edinburgh, in press.

KOETZNER, K. L., 1963. An ecological survey of the algae of Great South Bay, N. Y. *M.S. Thesis, University of Rhode Island,* Kingston, Rhode Island, 68 pp.

LIE, U., 1968. A quantitative study of benthic infauna in Puget Sound, Washington, U.S.A. in 1963–1964. *Fiskeridvi. Skr. Ser. Havunders,* **14** : 229–556.

MURAWSKI, W. S., 1969. A study of submerged dredge holes in New Jersey estuaries with respect to their fitness as finfish habitat. *New Jersey Div. Fish Game Misc. Rep.,* No. **2-M** : 1–32.

MYREN, R. T., 1964. A study of the effect of turbulence and oxygen in the estuarine environment. *Ph.D. thesis, Cornell University,* Ithaca, New York, 106 pp.

NASSAU-SUFFOLK REGIONAL PLANNING BOARD, 1966. The status and potential of the marine environment. (Summary available from: Nassau-Suffolk Regional Planning Board, Hauppauge, New York 11787.)

NICHOLS, M. M., 1964. Characteristics of sedimentary environment in Moriches Bay, N. Y. Pages 363–383 in R. L. Miller, Ed., *Papers in Marine Geology, Shepard Commemorative Volume.* MacMillan Company, New York.

ODUM, E. P., 1959. *Fundamentals of Ecology.* [2nd ed.] W. B. Saunders Company, Philadelphia, 546 pp.

ODUM, W. E., G. M. WOODWELL AND C. F. WURSTER, 1969. DDT residues absorbed from organic detritus by fiddler crabs. *Science,* **164** : 576–577.

PHELPS, D. K., 1964. Functional relationships of benthos in a coastal lagoon. *Ph.D. thesis, University of Rhode Island,* Kingston, Rhode Island, 146 pp.

PIELOU, E. C., 1966. Species-diversity and pattern-diversity in the study of ecological succession. *J. Theor. Biol.,* **10** : 370–383.

POWERS, C. F., AND A. ROBERTSON, 1967. Design and evaluation of an all-purpose benthos sampler. Pages 126–131 in J. C. Ayers and D. C. Chandler, Eds., *Studies on the Environment and Eutrophication of Lake Michigan, Special Report No. 30,* Great Lakes Research Division, University of Michigan.

RAYMONT, J. E. C., 1947. An experiment in fish cultivation: IV. The bottom fauna and the food of flatfishes in a fertilized sea-loch. (Loch Craiglin, Argyll). *Proc. Roy. Soc. Edinburgh Series B,* **63** : 34–44.

RAYMONT, J. E. C., 1949. Further observations on changes in the bottom fauna of a fertilized sea loch. *J. Mar. Biol. Ass. U. K.,* **28** : 9–19.

REISH, D. J., 1955. The relation of the polychaetous annelids to harbour pollution. *Pub. Health Rep.,* **70** : 1168–1174.

REISH, D. J., 1955. The relationship of the polychaetous annelid *Capitella capitata* (Fabricius) to waste discharges of biological origin. *U. S. Pub. Health Serv. Publ.,* **208** : 195–200.

REISH, D. J., 1959. An ecological study of pollution in Los Angeles–Long Beach Harbours, Calif. *Allan Hancock Found. Publ. Occas. Pap.,* **22** : 1–119.

RHOADS, D. C., AND D. K. YOUNG, 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.,* **28** : 150–178.

RYTHER, J. H., 1954. The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, N. Y. *Biol. Bull.,* **106** : 198–209.

SANDERS, H. L., 1956. Oceanography of Long Island Sound, 1952–1954. X. Biology of marine bottom communities. *Bull. Bingham Oceanogr. Coll.,* **15** : 345–414.

SANDERS, H. L., 1958. Benthic studies in Buzzards Bay. I. Animal sediment relationships. *Limnol. Oceanogr.,* **3** : 245–258.

SANDERS, H. L., 1968. Marine benthic diversity: A comparative study. *Amer. Natur.,* **102** : 243–282.

SHANNON, C. E., AND W. WEAVER, 1963. *The Mathematical Theory of Communication.* University of Illinois Press, Urbana, Illinois, 117 p.

SMITH, R. I., Ed., 1964. *Keys to Marine Invertebrates of the Woods Hole Region; A Manual.* Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts, 208 pp.

SOKAL, R. R., AND J. F. ROHLF, 1969. *Biometry.* W. H. Freeman and Company, San Francisco, 776 pp.

STAUFFER, R. C., 1937. Changes in the invertebrate community of a lagoon after disappearance of the eelgrass. *Ecology,* **18** : 427–431.

STRICKLAND, J. D. H., 1960. Measuring the production of marine phytoplankton, *Bull. Fish. Res. Board Can.,* **122** : 1–172.

TEAL, J. M., 1962. Energy flow in the salt marsh ecosystems of Georgia. *Ecology,* **43**: 614–624.

THOMAS, M. L. H., 1970. Studies on the benthos of Bideford River, Prince Edward Island. *Ph.D. thesis, Dalhousie University,* Halifax, Nova Scotia, 362 pp.

THORSON, G., 1957. Bottom communities. Pages 461–534 in J. W. Hedgepeth, Ed., *Treatise on Marine Ecology and Palaeoecology, Vol. I.* Waverly Press, Baltimore.

TOWNES, H. K., JR., 1939. Ecological studies on the Long Island marine invertebrates of importance as fish food or as bait. *Twenty-eighth Annual Report, 1938, State of New York Conservation Department,* No. **XIV** (Suppl.): 163–176.

UDELL, H. F., J. ZARUDSKY, T. E. DOHENY AND P. R. BURKHOLDER, 1969. Productivity and nutrient values of plants growing in the salt marshes of the Town of Hempstead, Long Island. *Bull. Torrey Bot. Club,* **96**: 42–51.

U. S. FEDERAL WATER POLLUTION CONTROL ADMINISTRATION, 1966a. *Proceedings Conference In the Matter of Pollution of Navigable Waters of Moriches Bay and the Eastern Section of Great South Bay and Their Tributaries, September 20–22, 1966.* U. S. GPO 0–242–427, Patchogue, New York, 496 pp.

U. S. FEDERAL WATER POLLUTION CONTROL ADMINISTRATION, 1966b. *Report on Pollution of the Navigable Waters of Moriches Bay and Eastern Section of Great South Bay, Long Island New York.* Hudson-Champlain and Metropolitan Coastal Comprehensive Water Pollution Control Project, Metuchen, New Jersey, 29 pp.

U. S. FEDERAL WATER POLLUTION CONTROL ADMINISTRATION, 1967. *Proceedings Conference Pollution of the Navigable Waters of Moriches Bay and the Eastern Section of Great South Bay and Their Tributaries, June 21, 1967.* U. S. GPO 957–639, Patchogue, New York, 134 pp.

U. S. FEDERAL WATER POLLUTION CONTROL ADMINISTRATION, 1968. *National Estuarine Pollution Study, July 23, 1968.* Proc. Public Mtg., New York, New York., 535 pp.

U. S. PRESIDENT'S SCIENCE ADVISORY COMMITTEE, ENVIRONMENTAL POLLUTION PANEL, 1965. Restoring the quality of our environment. The White House, 1965. (Available from: Superintendent of Documents, GPO, Washington, D.C. 20420).

WESTLAKE, D. F., 1963. Comparisons of plant productivity. *Biol. Rev.* **38**, 385–425.

WOODWELL, G. M., C. F. WURSTER, JR. AND P. A. ISAACSON, 1967. DDT residues in an east coast estuary: A case of biological concentration of a persistent pesticide. *Science,* **156**: 821–824.

YENTSCH, C. S., 1963. Primary Production. Pages 157–175 in H. Barnes, Ed., *Annual Review of Oceanography and Marine Biology, Vol. 1.* George Allen and Unwin, Ltd., London.